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Analysing the European genera of family Lestidae (Odonata: Zygoptera) with special emphasis on the status of Chalcolestes based on the morphological characteristics of male adults

Csilla Vajda[a*], László József Szabó[a], Csaba Cserháti[b] and György Dévai[a]

[a]*Department of Hydrobiology, Institute of Biology and Ecology, Faculty of Science and Technology, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary;* [b]*Department of Solid State Physics, Institute of Physics, Humanities and Sciences, Faculty of Science and Technology, University of Debrecen, Bemtér 18/b, H-4026 Debrecen, Hungary*

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Lestidae is a heterogeneous family with more than 150 species worldwide. There are many debates concerning its resolution. One of them is whether the genus *Chalcolestes* should be recognized as a genus or considered as a synonym of *Lestes*. We compared male characteristics of eight Hungarian species of three genera (*Lestes*, *Chalcolestes* and *Sympecma*) of the family Lestidae to get closer to the answer. We analysed the morphometry of genital and non-genital characteristics and the morphology of the secondary genitalia, especially the ligula. The morphometric analyses showed that two *Chalcolestes* species were the biggest in the most of the cases while *Sympecma fusca* (Vander Linden, 1820) and *Lestes virens* (Charpentier, 1825) were the smallest. The genera were separated mainly by the genitalic traits in the morphometric analyses. The differences in the secondary genitalia strengthen the generic status of *Chalcolestes*.

Keywords: Odonata; dragonfly; *Lestes*; *Chalcolestes*; *Sympecma*; secondary genitalia; ligula; genital and non-genital characters

Introduction

The superfamily Lestoidea Calvert it is the sister group of all other Zygoptera (Bybee, Ogden, Branham, & Whiting, 2008; Carle, Kjer, & May, 2008; Davis, Nicholson, Saunders, & Mayhew, 2011; Dumont, Vierstraete, & Vanfleteren, 2010). Lestidae Calvert, 1901 is a heterogeneous family of Odonata with 153 species (Schorr & Paulson, 2017) worldwide (cf. table 2 in Jödicke, 1997) classified currently in nine genera (Schorr & Paulson, 2017). The resolution of the family is not completed yet. As we know the family is monophyletic (Bybee et al., 2008; Dijkstra, Kalkman, Dow, Stokvis, & Van Tol, 2014; Rehn, 2003). Only three genera with nine species (Boudot & Kalkman, 2015; Kalkman et al., 2010) of Lestidae are represented in Europe: *Chalcolestes* Kennedy, 1920 [*Chalcolestes parvidens* (Artobolevsky, 1929); *Chalcolestes viridis* (Vander Linden, 1825)], *Lestes* Leach [*Lestes barbarus* (Fabricius, 1798); *Lestes dryas* Kirby, 1890; *Lestes macrostigma* (Eversmann, 1836); *Lestes sponsa* (Hansemann, 1823); *Lestes virens* (Charpentier, 1825)] and *Sympecma* Burmeister [*Sympecma fusca* (Vander Linden, 1820); *Sympecma*

*Corresponding author. Email: vajda.csilla@science.unideb.hu

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paedisca (Brauer, 1877)]. Concerning their morphology, ecology and distribution Jödicke (1997) published a comprehensive monograph.

The three genera can be separated well from each other. The genus *Sympecma* is distinguished from the two others by resting the wings closed above the abdomen instead of resting with half-opened wings. Furthermore, *Sympecma* species have buff markings with glossy brown colour while *Lestes* and *Chalcolestes* species have colour from metallic green to copper red with bluish pruinosity. *Sympecma* is also differentiated by the location of the pterostigma, which is closer to the tip of the wing in forewings than in hind wings instead of being located at the same distances. Behavioural differences are also conspicuous, as *Sympecma* species overwinter as imagos instead of eggs. *Chalcolestes* species differ from *Lestes* in the prementum of the larvae. It is rather broad basally, instead of narrowed. Furthermore, *Chalcolestes* species have a spur-like longitudinal green spot on the metepisternum, marking the lower border of the green area. Moreover, their behaviour also differs. Females of the genus *Chalcolestes* oviposit in living wood, although Lopau (1996 cit. Olias et al., 2007) reported an exception from Greece, where *C. parvidens* emerged from *Bolboschoenus maritimus* and later observed emergences in Corfu and Zakynthos in water areas without woody plants (Lopau, 2006 cit. Olias et al., 2007).

Furthermore, the newest genetic investigations (Dijkstra & Kalkman, 2012; Dumont et al., 2010; Gyulavári et al., 2011; Samraoui, 2009) demonstrated that *Chacolestes* is nearer to *Sympecma* than to the true *Lestes* and should be considered at the genus level. They were followed by many authors (Grand & Boudot, 2006; Hardersen, 2004; Hardersen & Dal Cortivo, 2008; Holzinger, Chovanec, & Waringer, 2015; Šácha et al., 2014; Schorr & Paulson, 2017; Skvortsov, 2010).

Nevertheless the genus name *Chalcolestes* has not been generally accepted since Kennedy erected it to accommodate *Lestes viridis* (Kennedy, 1920a). In many frequently used field guides (Askew, 1988; d'Aguilar, Dommanget, & Préchac, 1986; Dijkstra & Lewington, 2006) the genus *Lestes* is still used for *viridis* and *parvidens* whether they are treated as species or subspecies, thus influencing faunistic works and species lists (Buczynski & Moroz, 2008; De Knijf, Vanappelghem, & Demolder, 2013; Jovic, Andjus, & Santovac, 2009; Jovic, Gligorovic, & Stankovic, 2010; Kalkman et al., 2010; Olias & Guenther, 2005; van Tol, 2016) and other research papers (Agüero-Pelegrin, Ferreras-Romero, & Corbet, 1999; Corbet, 1999; De Block, Geenen, Jordaens, Backeljau, & Stoks, 2005; Geenen, Jordaens, De Block, Stoks, & De Bruyn, 2000; Samraoui, 2009; Willkommen, Dreyer, & Gorb, 2014). Also, some authors treat *Chalcolestes* as a subgenus of *Lestes* and use the name as *Lestes* (*Chalcolestes*) *viridis* (e.g. Jödicke, 1997; Raab, Chovanec, & Pennerstorfer, 2007).

Consequently, our aim was to compare morphologically the three existing genera of the family Lestidae in Hungary, and to characterize the differences we might detect. For the comparison non-genital and genital characters were used on male adults from Hungarian populations.

Materials and methods

For the comparison 198 male adults were included from 12 Hungarian populations of the eight Hungarian species of the family Lestidae. We used data from earlier descriptions of eight populations (Kis et al., 2012, 2013, 2014; Nagy, Vajda, Szabó, Miskolczi, & Dévai, 2012; Vajda, Szabó, Miskolczi, Cserháti, & Dévai, 2013; Vajda, Szabó, Miskolczi, & Dévai, 2011, 2015a; Vajda, Vincze, Szabó, Miskolczi, & Dévai, 2015b) in addition to our previously unpublished data from four NE-Hungarian populations.

In the former works 21 body traits were measured: nine non-genital traits and 12 genital traits. For better understanding formerly used Hungarian abbreviations were replaced with English ones (indicated as HUN = EN). Non genital traits were the body length (Tth = BL), the abdomen

length (Pth = AL), five characters on the head (Fs = HW – width of the head; SZkt = CED – distance between the compound eyes measured on the line of HW; CSTkt = ScD – distance between the two scapi; UFszkt = PCW – width of the postclypeus measured on the upper carina; FAs = LW – width of the labrum), two characters on the right third leg (J3LCh = R3LFL – the length of the femur; J3LLh = R3LTL – the length of the tibia). The genital traits were between distinctive points of the lower and upper appendages of the abdomen end [six characters in each side (Left: PVK1–6B = Abd1–6L, Right: PVK1–6J = Abd1-6R)], see figure 2 in Vajda et al. (2011). During the comparison original data were used in case of body length, abdomen length, traits of the head and of the leg but not in the case of the abdominal end where the mean of the two sides was used at particular cases respectively (e.g. PVK1 = (PVK1J + PVK1B)/2). Measurements were taken with a digital calliper (to the nearest 0.01 mm) and stereo microscopes (Zeiss SMXX and Zeiss Techinval, Zeiss, Jena, Germany) with ocular micrometers.

For the statistical analysis box plots were produced to show quantiles of each variable. While the data were normally distributed (Shapiro–Wilk test) the species were compared with ANOVA with Tukey's pairwise comparisons for all the features. Prior to the multivariate statistical analyses we used square root transformation to normalize the data. For the multivariate analysis the body and abdomen lengths (BL and AL characters) were excluded, because they would have distorted the results. Species were compared with MANOVA and canonical variation analysis (CVA). Cluster analyses were performed to clarify the morphological similarity among the species. We used the functions at group centroids from CVA (Ward's algorithm). Additionally regression tree analyses were performed to the species of the *Lestes* genus to identify traits that best discriminated species.

Multivariate tests were run separately for the non-genital and genital characters as well as for all characters.

Statistical analyses were performed using PAST version 2.17 (Hammer, Harper, & Ryan, 2001), SPSS ver. 22.0 and R programme package (R Development Core Team, 2010).

The morphology of the secondary genitalia (especially the ligula) in selected specimens was studied as well. We used a scanning electron microscope (Hitachi S-4300 CFE, Hitachi, Tokyo, Japan) at 5 kW and light microscope (Olympus SZX16, Olympus, Tokyo, Japan). For the SEM investigations the appropriate part of the abdomen was cut off and the penis was twisted out from under the vesicula spermalis. Specimens were dehydrated in a series of alcohol (two times 24 hours in 96% alcohol in refrigerator, then 24 hours in absolute alcohol in room temperature). After dehydrating, specimens were fixed on specimen holders and dried in a drying cabinet for another 24 hours at 80°C. To avoid charges under the electron beam a thin gold layer was evaporated onto the free surfaces.

Results

Non-genital traits

According to ANOVA, there were significant ($p < 0.001$) differences among the species (Table 1). The *Chalcolestes* species had the longest body and abdomen length (Table 2, Figure 1) and a clear trend was found for these traits between the species in an ascending order: *S. fusca*, *L. virens*, *L. sponsa*, *L. macrostigma*, *L. barbarus*, *L. dryas*, *C. viridis*, *C. parvidens*. Other traits do not follow this trend. *L. dryas* was markedly larger in traits of the head, especially HW, CED, ScD, LW (Table 2, Figure 1) than the others. *Sympecma fusca* which was the smallest in body length proved to have an average value for the traits ScD and PCW. On the basis of the traits of the third right leg (R3LFL, R3LTL) three groups could be divided: (i) *S. fusca*, *L. virens*, (ii) *C. parvidens*, *C. viridis*, *L. sponsa*, (iii) *L. macrotigma*, *L. barbarus*, *L. dryas*.

Table 1. Differences between species (ANOVA) for the 15 morphometric characters.

		Sum of Squares	df	Mean Square	F	Sig.
BL	Between groups	1544.49	7	220.64	139.30	< 0.001
	Within groups	300.99	190	1.58		
	Total	1845.48	197			
AL	Between groups	1071.21	7	153.03	123.30	< 0.001
	Within groups	235.90	190	1.24		
	Total	1307.11	197			
HW	Between groups	25.99	7	3.71	246.60	< 0.001
	Within groups	2.86	190	0.02		
	Total	28.85	197			
CED	Between groups	11.07	7	1.58	260.90	< 0.001
	Within groups	1.15	190	0.01		
	Total	12.22	197			
ScD	Between groups	3.46	7	0.49	181.10	< 0.001
	Within groups	0.52	190	0.00		
	Total	3.98	197			
PCW	Between groups	2.33	7	0.33	68.74	< 0.001
	Within groups	0.92	190	0.00		
	Total	3.25	197			
LW	Between groups	3.49	7	0.50	220.60	< 0.001
	Within groups	0.43	190	0.00		
	Total	3.92	197			
R3LFL	Between groups	40.27	7	5.75	167.20	< 0.001
	Within groups	6.54	190	0.03		
	Total	46.80	197			
R3LTL	Between groups	64.30	7	9.19	168.30	< 0.001
	Within groups	10.37	190	0.05		
	Total	74.67	197			
Abd1	Between groups	1.60	7	0.23	88.56	< 0.001
	Within groups	0.49	190	0.00		
	Total	2.09	197			
Abd2	Between groups	1.33	7	0.19	127.60	< 0.001
	Within groups	0.28	190	0.00		
	Total	1.61	197			
Abd3	Between groups	1.25	7	0.18	125.60	< 0.001
	Within groups	0.27	190	0.00		
	Total	1.51	197			
Abd4	Between groups	2.48	7	0.35	65.68	< 0.001
	Within groups	1.03	190	0.01		
	Total	3.51	197			
Abd5	Between groups	1.75	7	0.25	122.50	< 0.001
	Within groups	0.39	190	0.00		
	Total	2.14	197			
Abd6	Between groups	6.54	7	0.93	278.90	< 0.001
	Within groups	0.64	190	0.00		
	Total	7.18	197			

MANOVA showed significant differences among the species (Wilk's lambda: 0.0007; df1 = 49; df2 = 938.6; F = 61.55; $p < 0.001$). Pairwise comparison showed also a significant difference in all cases ($p < 0.001$).

The first two axes of CVA explained 75.58% of total variance. The first axis was determined by the CED and ScD traits and the second axis by PCW, HW, R3LFL and R3LTL traits. Along the first axis (Figure 2) *L. dryas* and *L. barbarus* were separated from others mainly in the sizes of the leg. Along the second axis *Chalcolestes* species and *L. sponsa* were separated from other

Table 2. Range of the measurements (in mm) of the non-genital characters. (CIL: confident interval lower limit, CIU: confident interval upper limit, SD: standard deviation, N: number of specimens).

		BL	AL	HW	CED	ScD	PCW	LW	R3LFL	R3LTL
L. macrostigma (N = 14)	Mean	41.57	33.52	4.98	2.55	1.51	1.05	1.26	4.52	5.08
	CIL	40.51	32.45	4.82	2.51	1.48	1.03	1.24	4.46	5.01
	CIU	42.63	34.59	5.02	2.59	1.53	1.07	1.28	4.58	5.16
	SD	1.835	1.849	0.062	0.074	0.041	0.030	0.030	0.103	0.131
L. sponsa (N = 15)	Mean	39.65	31.54	4.88	2.49	1.38	0.95	1.18	4.90	5.41
	CIL	39.04	31.02	4.82	2.44	1.36	0.93	1.16	4.80	5.29
	CIU	40.27	32.06	4.95	2.54	1.41	0.98	1.20	5.01	5.54
	SD	1.119	0.942	0.118	0.088	0.045	0.050	0.031	0.185	0.220
L. virens (N = 35)	Mean	36.71	29.20	4.73	2.36	1.34	0.89	1.12	3.92	4.31
	CIL	36.09	28.65	4.67	2.33	1.32	0.87	1.10	3.86	4.23
	CIU	37.34	29.74	4.78	2.39	1.36	0.92	1.14	3.98	4.38
	SD	1.812	1.585	0.157	0.093	0.067	0.071	0.058	0.176	0.224
L. barbarus (N = 34)	Mean	41.63	32.65	5.27	2.67	1.50	1.00	1.41	4.86	5.41
	CIL	41.13	32.25	5.22	2.64	1.48	0.97	1.39	4.79	5.32
	CIU	42.13	33.06	5.33	2.70	1.51	1.04	1.43	4.94	5.50
	SD	1.438	1.156	0.152	0.082	0.053	0.105	0.054	0.216	0.250
L. dryas (N = 55)	Mean	42.61	33.47	5.63	2.95	1.68	1.19	1.47	5.09	5.72
	CIL	42.40	33.27	5.59	2.93	1.67	1.17	1.45	5.02	5.64
	CIU	42.83	33.67	5.66	2.97	1.69	1.21	1.48	5.15	5.80
	SD	0.793	0.753	0.120	0.083	0.049	0.066	0.053	0.230	0.296
C. viridis (N = 15)	Mean	44.28	35.66	5.12	2.45	1.38	1.10	1.29	4.27	4.78
	CIL	43.82	35.22	5.07	2.42	1.35	1.08	1.27	4.22	4.69
	CIU	44.73	36.10	5.18	2.48	1.40	1.11	1.31	4.32	4.88
	SD	0.827	0.795	0.099	0.050	0.038	0.033	0.031	0.087	0.173
C. parvidens (N = 15)	Mean	45.08	36.49	5.21	2.41	1.39	1.14	1.28	4.36	4.66
	CIL	44.61	36.12	5.18	2.40	1.39	1.12	1.27	4.31	4.59
	CIU	45.55	36.85	5.23	2.43	1.40	1.16	1.29	4.42	4.74
	SD	0.844	0.656	0.047	0.029	0.018	0.041	0.015	0.100	0.132
S. fusca (N = 15)	Mean	36.51	28.66	4.56	2.34	1.39	1.07	1.20	4.05	4.21
	CIL	36.13	28.37	4.53	2.31	1.35	1.03	1.17	3.98	4.13
	CIU	36.88	28.96	4.60	2.37	1.43	1.11	1.22	4.12	4.29
	SD	0.672	0.532	0.070	0.054	0.070	0.070	0.042	0.127	0.144

species, also mainly in the sizes of leg. The convex hulls for the first two axis overlapped to a great extent. Nonetheless, according to the first seven canonical function the clustering efficiency was 96.97%. Six specimens were misclassified.

Cluster analysis for centroids (Figure 3) differentiated two main branches: (i) *L. sponsa*, *S. fusca*, *L. macrostigma*, *L. virens*; and (ii) *L. barbarus*, *L. dryas*, *C. viridis*, *C. parvidens*. The sub-branches clustered together *C. viridis* and *C. parvidens* as well as *L. barbarus* with *L. dryas* and, surprisingly, *L. macrostigma* with *L. virens*.

The regression tree analysis (Figure 4) separated *L. dryas* and *L. barbarus* based on LW trait. The others were clustered in two branches (i) *L. virens*, *S. fusca*; and (ii) *L. sponsa*, *L. macrostigma*, *C. parvidens*, *C. viridis* which were divided by the R3LFL. A *L. macrostigma* specimen was uninvolved in the *L. sponsa*–*L. macrostigma* branch because of its size and clustered to the sub-branch of *Chalcolestes* species.

Genital traits

Significant differences were between the species – according to ANOVA – ($p < 0.001$) in each trait (Table 1). The Abd1 and Abd2 characters were remarkably smaller in *S. fusca*, *L. virens* and *L. sponsa* than in others (Table 3, Figure 5). The values of Abd3 were strikingly larger in *L.*

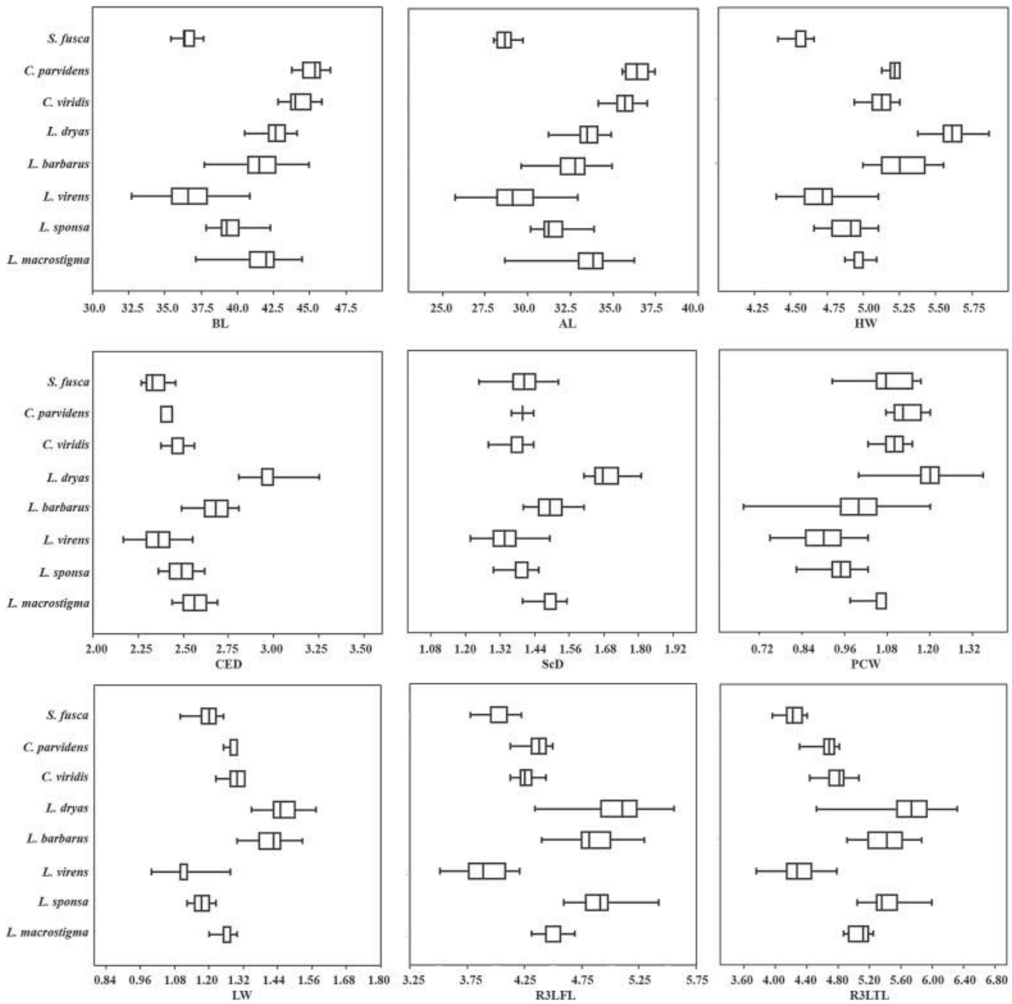

Figure 1. Box plots for non-genital characters.

dryas, while the others were similar to each other (Figure 5). Abd4 was smallest in *S. fusca* and *L. virens*, largest in *L. macrostigma* and *L. dryas* but had a very high standard deviation in the latter. The Abd5 was the smallest in the two *Chalcolestes* species (Figure 5). The best separation of the species was in the case of Abd6 trait. Based on the latter the species could be divided into four groups from smallest to largest: (i) *L. sponsa*, *L. dryas*; (ii) *L. virens*, *L. barbarus*; (iii) *S. fusca*, *C. parvidens*, *C. viridis*; and (iv) *L. macrostigma* (Figure 5).

MANOVA separated the species significantly (Wilk's lambda: 0.0005; df1 = 42; df2 = 871.2; F = 83.88; $p < 0.001$), as did the pairwise comparisons ($p < 0.001$).

The first two axes of CVA explained 87.87% of all variation. The first axis was determined mainly by the Abd3, Abd5, Abd6 traits and the second one by Abd1 Abd2 and Abd4 traits. Species separated well along the first two axis (Figure 6). Only *L. barbarus* and *L. macrostigma* overlapped to a great extent. *L. sponsa* and *L. dryas* completely separated from others along the first axis and from each other along the second axis. *Chalcolestes* species were separated from others also on the first axis, mainly based on the Abd6 trait. The classification efficiency was 97.47%. Five specimens were misclassified.

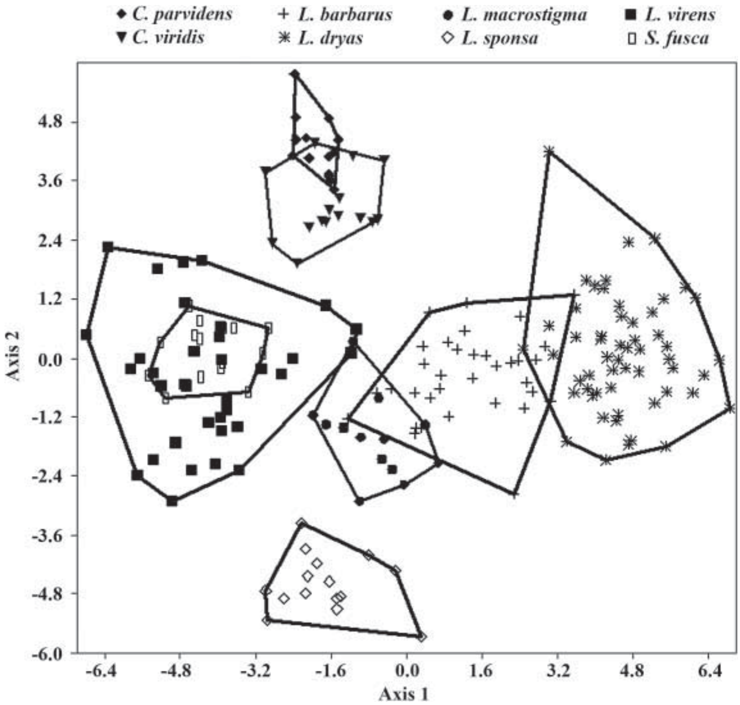

Figure 2. Canonical variates analysis (CVA) for non-genital characters.

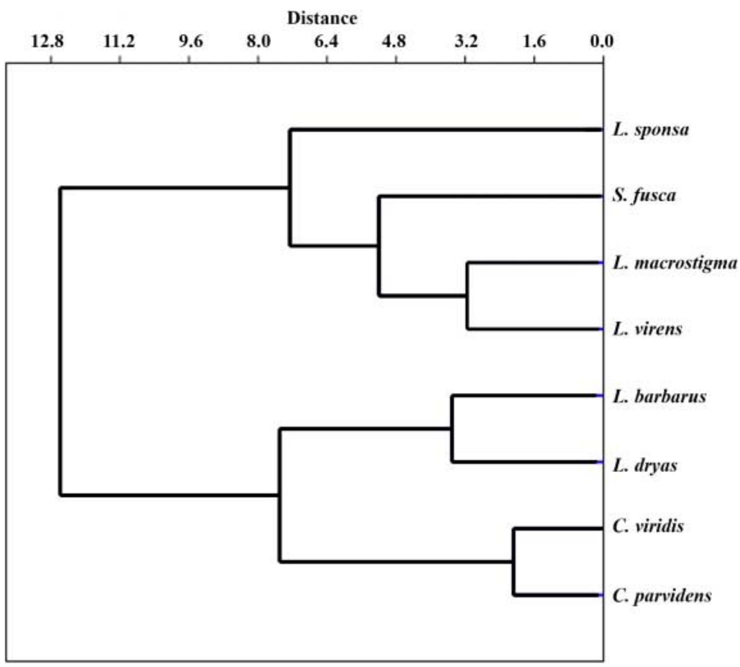

Figure 3. Cluster analysis (Ward's algorithm) for the functions at group centroids of CVA for measurements of non-genital characters.

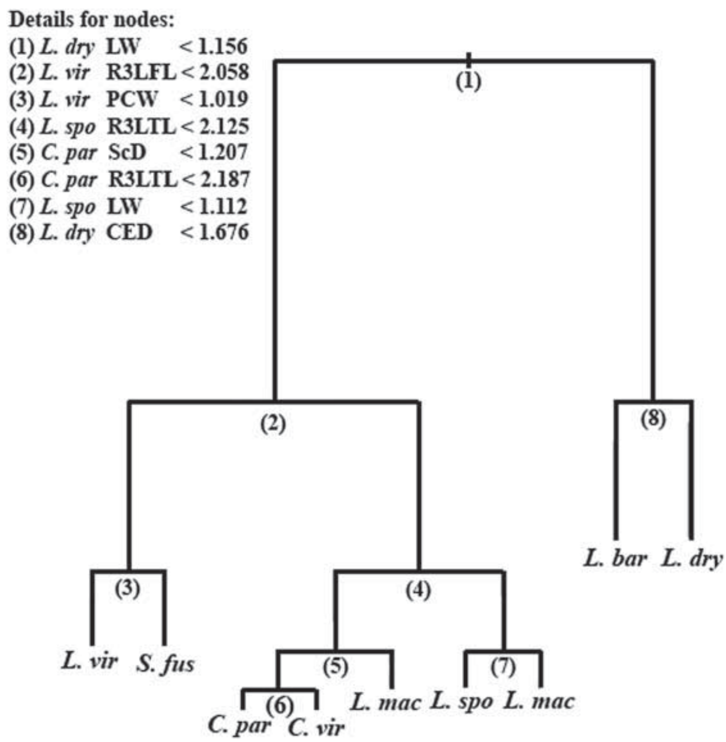

Figure 4. Regression tree analysis based on the non-genital characters with the differentiating characters in each node and the cut-off values (in mm) identified by regression tree analysis that divide the dataset into two.

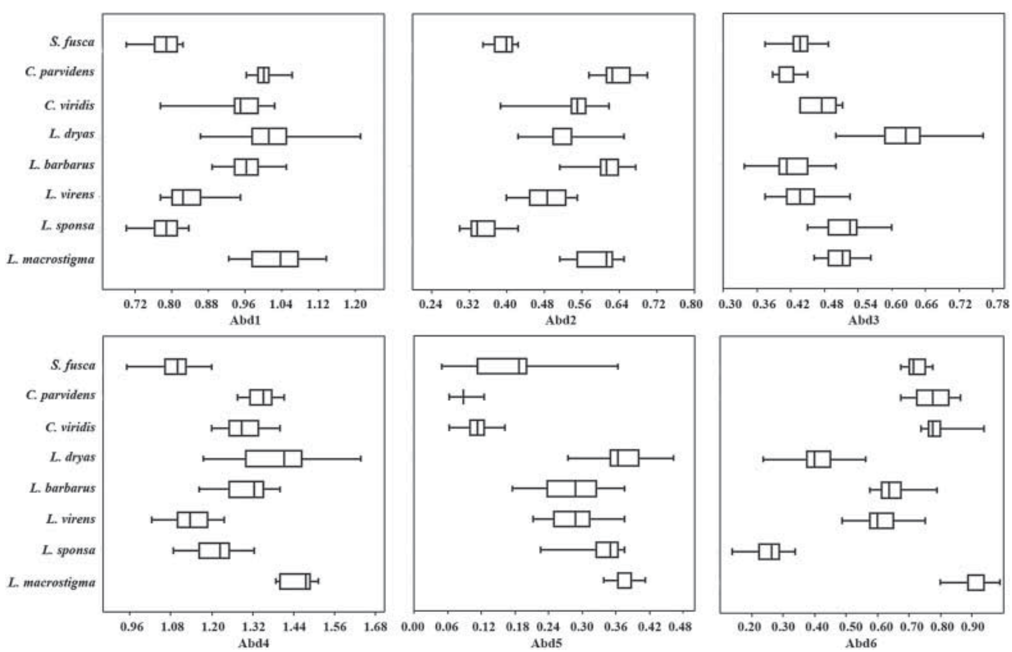

Figure 5. Box plots for genital characters.

Table 3. Range of the measurements (in mm) of genital characters. (CIL: confident interval lower limit, CIU: confident interval upper limit, SD: standard deviation, N: number of specimens).

		Abd1	Abd2	Abd3	Abd4	Abd5	Abd6
L. macrostigma (N = 15)	Mean	1.03	0.59	0.51	1.45	0.37	0.91
	CIL	1.00	0.57	0.49	1.43	0.36	0.88
	CIU	1.07	0.62	0.52	1.48	0.38	0.94
	SD	0.061	0.043	0.027	0.043	0.021	0.053
L. sponsa (N = 15)	Mean	0.78	0.35	0.52	1.21	0.34	0.25
	CIL	0.76	0.33	0.50	1.17	0.32	0.22
	CIU	0.80	0.37	0.54	1.24	0.36	0.28
	SD	0.037	0.032	0.037	0.062	0.039	0.059
L. virens (N = 35)	Mean	0.83	0.48	0.44	1.14	0.28	0.61
	CIL	0.82	0.47	0.43	1.12	0.27	0.59
	CIU	0.85	0.50	0.46	1.16	0.30	0.63
	SD	0.045	0.040	0.038	0.056	0.042	0.064
L. barbarus (N = 34)	Mean	0.97	0.61	0.42	1.30	0.28	0.65
	CIL	0.95	0.60	0.41	1.28	0.26	0.63
	CIU	0.98	0.63	0.43	1.32	0.30	0.67
	SD	0.040	0.036	0.040	0.063	0.052	0.053
L. dryas (N = 55)	Mean	1.01	0.51	0.62	1.39	0.37	0.41
	CIL	0.99	0.50	0.60	1.36	0.36	0.39
	CIU	1.03	0.52	0.63	1.42	0.39	0.43
	SD	0.065	0.039	0.045	0.104	0.044	0.063
C. viridis (N = 15)	Mean	0.95	0.54	0.47	1.30	0.11	0.79
	CIL	0.91	0.52	0.46	1.27	0.10	0.76
	CIU	0.98	0.57	0.49	1.33	0.13	0.82
	SD	0.059	0.052	0.027	0.057	0.028	0.052
C. parvidens (N = 15)	Mean	1.00	0.63	0.42	1.35	0.09	0.78
	CIL	0.99	0.61	0.41	1.32	0.08	0.74
	CIU	1.01	0.65	0.43	1.37	0.10	0.81
	SD	0.025	0.036	0.019	0.040	0.015	0.059
S. fusca (N = 15)	Mean	0.78	0.39	0.44	1.09	0.18	0.72
	CIL	0.76	0.38	0.42	1.06	0.13	0.70
	CIU	0.80	0.40	0.45	1.13	0.23	0.74
	SD	0.034	0.022	0.030	0.066	0.082	0.032

Cluster analysis for centroids (Figure 7) separated clearly *L. sponsa* and *L. dryas* from others. The two *Chalcolestes* were clustered together as well as *L. virens* with *S. fusca* and *L. barbarus* with *L. macrostigma*.

The regression tree analysis (Figure 8) separated the *L. dryas* and *L. sponsa* from the others based on the Abd6 trait. The other species formed two sub-branches. One consists of *S. fusca* and the *Chalcolestes* species and they were separated by Abd4 trait. In the other sub-branch *L. macrostigma* was separated from *L. virens* and *L. barbarus* by Abd6 trait.

All traits

MANOVA significantly separated the species (Wilk's lambda: 7.983E-06; df1 = 95; df2 = 1118; F = 68.48; $p < 0.001$). The pairwise comparisons also showed significant differences between species pairs ($p < 0.001$).

Classification efficiency of CVA was 100%. However, according to the first two axes (explaining the 78.13% of total variance) there were overlaps between the convex hulls (Figure 9). Three groups separated along the first axis (i) *L. dryas*, *L. sponsa*; (ii) *L. barbarus*, *L. macrostigma*, *L. virens*, *S. fusca*; and (iii) *C. viridis*, *C. parvidens*. The two *Chalcolestes* species differ mainly in

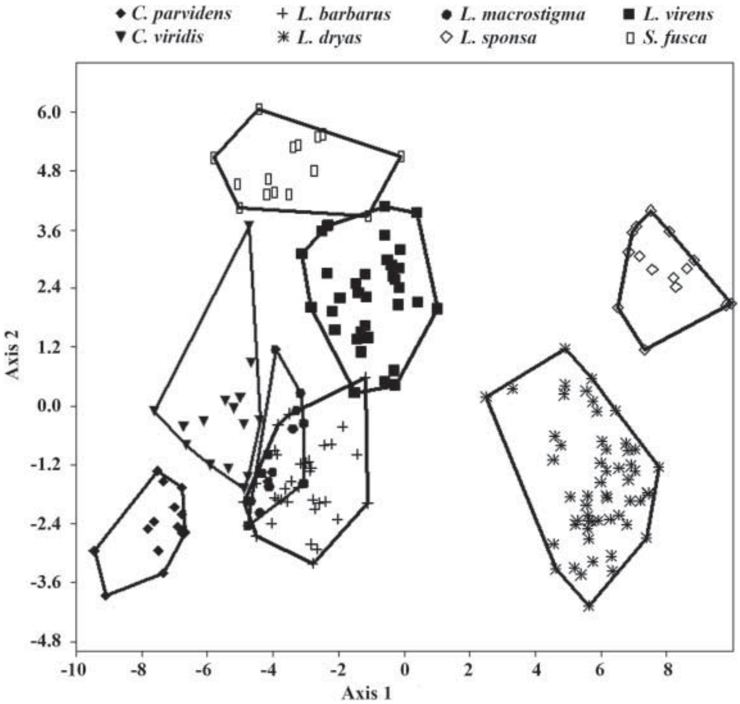

Figure 6. Canonical variates analysis (CVA) for genital characters.

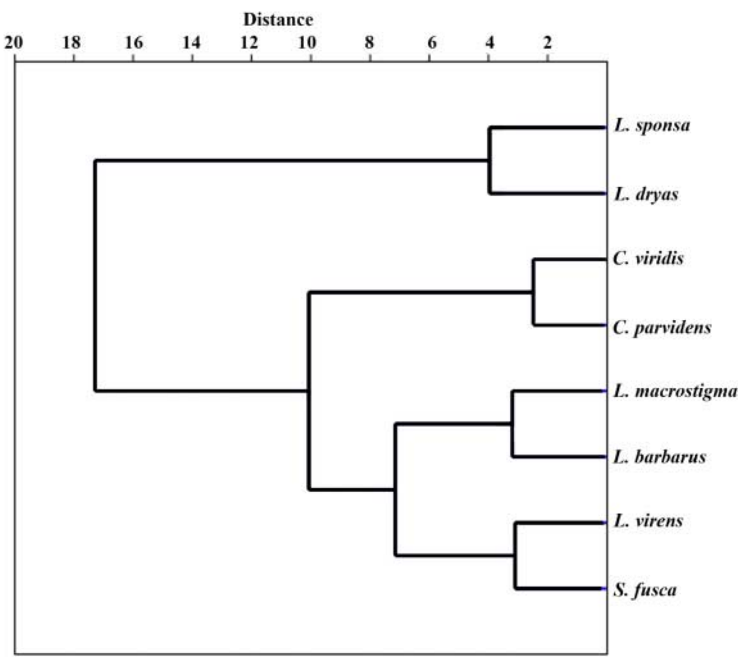

Figure 7. Cluster analysis (Ward's algorithm) for the functions at group centroids of CVA for measurements of genital characters.

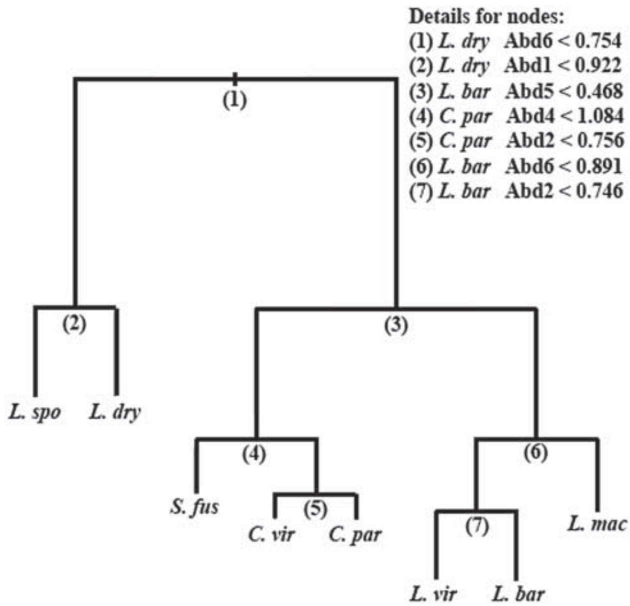

Figure 8. Regression tree analysis based on the genital characters with the differentiating characters in each node and the cut-off values (in mm) identified by regression tree analysis that divide the dataset into two.

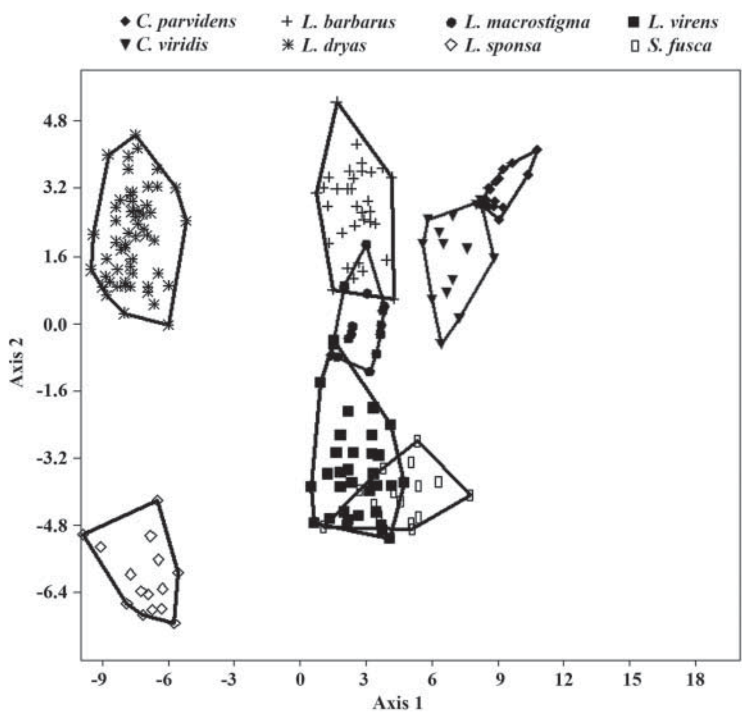

Figure 9. Canonical variates analysis (CVA) for all measurements (non-genital and genital characters together).

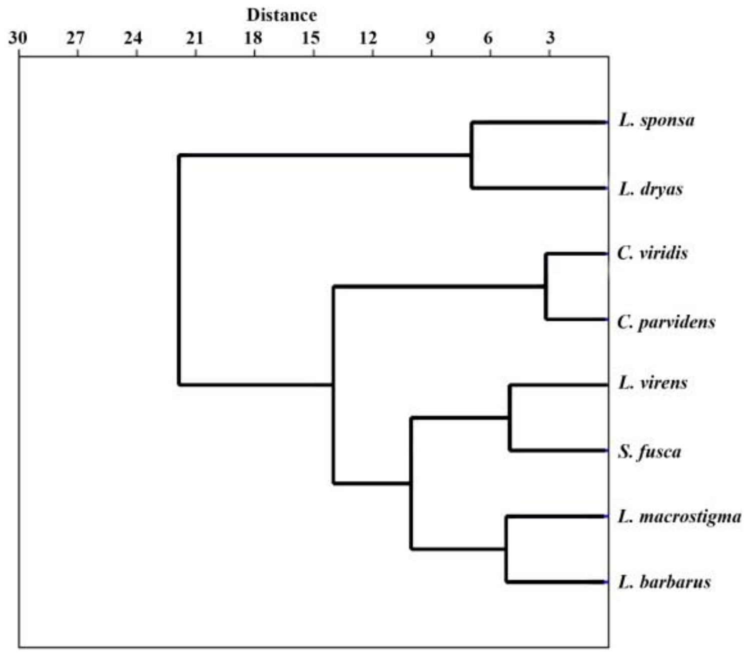

Figure 10. Cluster analysis (Ward's algorithm) for functions at group centroids from CVA for all measurements (non-genital and genital characters together).

the size of Abd5 and Abd6 from each other as well as from other species along the first axis. Along the second axis, species differentiated mainly in the size of R3LTL and HW.

The cluster analysis for centroids (Figure 10) separated *L. sponsa* with *L. dryas* far from the other six species. The two *Chalcolestes* were clustered together as was *L. virens* with *S. fusca* and *L. barbarus* with *L. macrostigma*.

The regression tree (Figure 11) separated in the first place *L. dryas* and *L. barbarus* from the other species based on the LW trait (Figure 11). The others were divided into two sub-branches based on the trait Abd5: (i) *S. fusca*, *C. viridis*, *C. parvidens*; (ii) *L. virens*, *L. sponsa*, *L. macrostigma*. All species were correctly divided by the test.

Morphological characterization of the secondary copulatory organ

The secondary copulatory organ (Figures 12, 13) showed little differences between species. The distal edge of the lamina batilliformis had pili (Figure 12b) in the case of *Chalcolestes* sp. but not in others (Figure 13e). The anterior processus of hamuli anteriores (Figures 12a, d, e, 13c, d, h) seemed to be longer and more slender in the case of *Chalcolestes* sp. than in *Lestes* sp. and *S. fusca*.

The ligula (Figures 12c, f, 13a, j, f) was spoon-like in all species. Its first segment, the prophallus, bore conspicuous lobes laterally in case of the two *Chalcolestes* species (Figure 12a, c, d). The chitin stem branches extended to the tip of the glans in the two *Chalcolestes* species, fusing with the terminal shelf (Figure 12c), but less elongated in the five *Lestes* species (Figure 13a, f, j) and *S. fusca* (Figure 12f). A paired lobe, lateral to the chitin stem branches was well developed in the two *Chalcolestes* species (Figure 12c), less developed in *S. fusca* (Figure 12f) and was barely visible or non-existent in the five *Lestes* species (Figure 13a, f, j).The five *Lestes* species bore a lobe (hood) in the middle of the glans at the end of the chitin stem branches (Figure 13a, f, g, i–k), which was split open in *S. fusca* (Figure 12f) but missing in the two *Chalcolestes* species

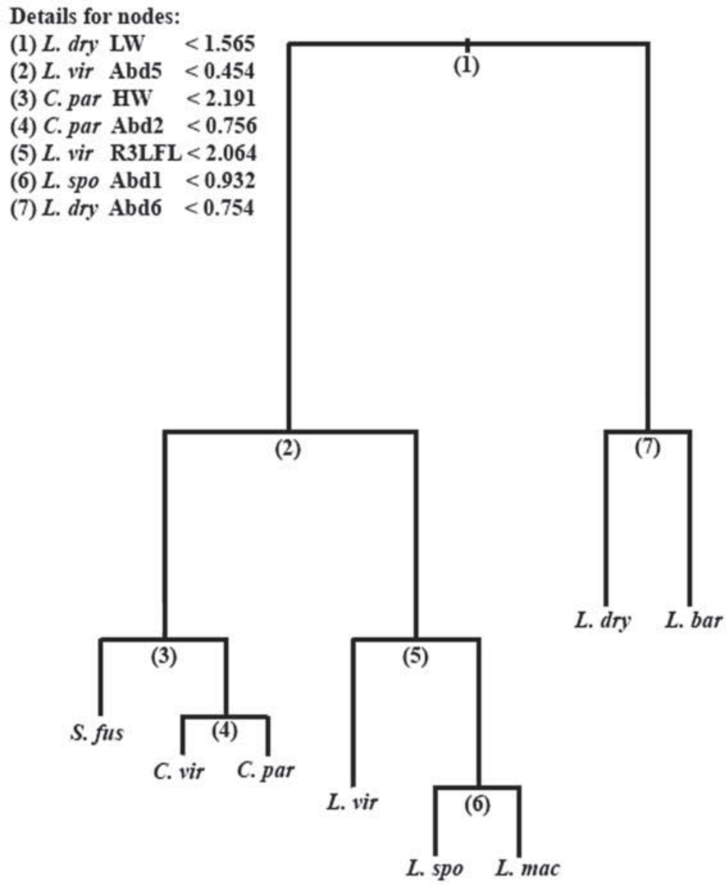

Figure 11. Results of regression tree analysis based on all characters with the differentiating characters in each node and the cut-off values (in mm) identified by regression tree analysis that divide the dataset into two.

(Figure 12c). This hood can be wide (*L. sponsa*, *L. dryas*) or narrow (*L. macrostigma*, *L. virens*) for its full length or can have a wide base with narrowing end (*L. barbarus*). The terminal shelf bore a long paired horn-like structure presented in the two *Chalcolestes* species (Figure 12c) which was less developed in other cases (Figures 12f, 13a, d, f, i, j).

Discussion

The three genera could not be separated clearly with the multivariate analyses. The main differences came from the larger size of *Chalcolestes* species and the smaller size of *S. fusca*. *L. sponsa* and *L. dryas* clearly separated from the others by the traits of the abdomen end especially the length of the lower appendages. *L. virens* and *S. fusca* have similar small bodies, heads, legs and abdomen ends. The similarity of *L. macrostigma* and *L. virens* in the traits of the head is remarkable.

Also noticeable is that the analysis for genital characters have the same results as the analysis including all traits. This can mean a greater significance of genital characters in the analyses than non-genital characters.

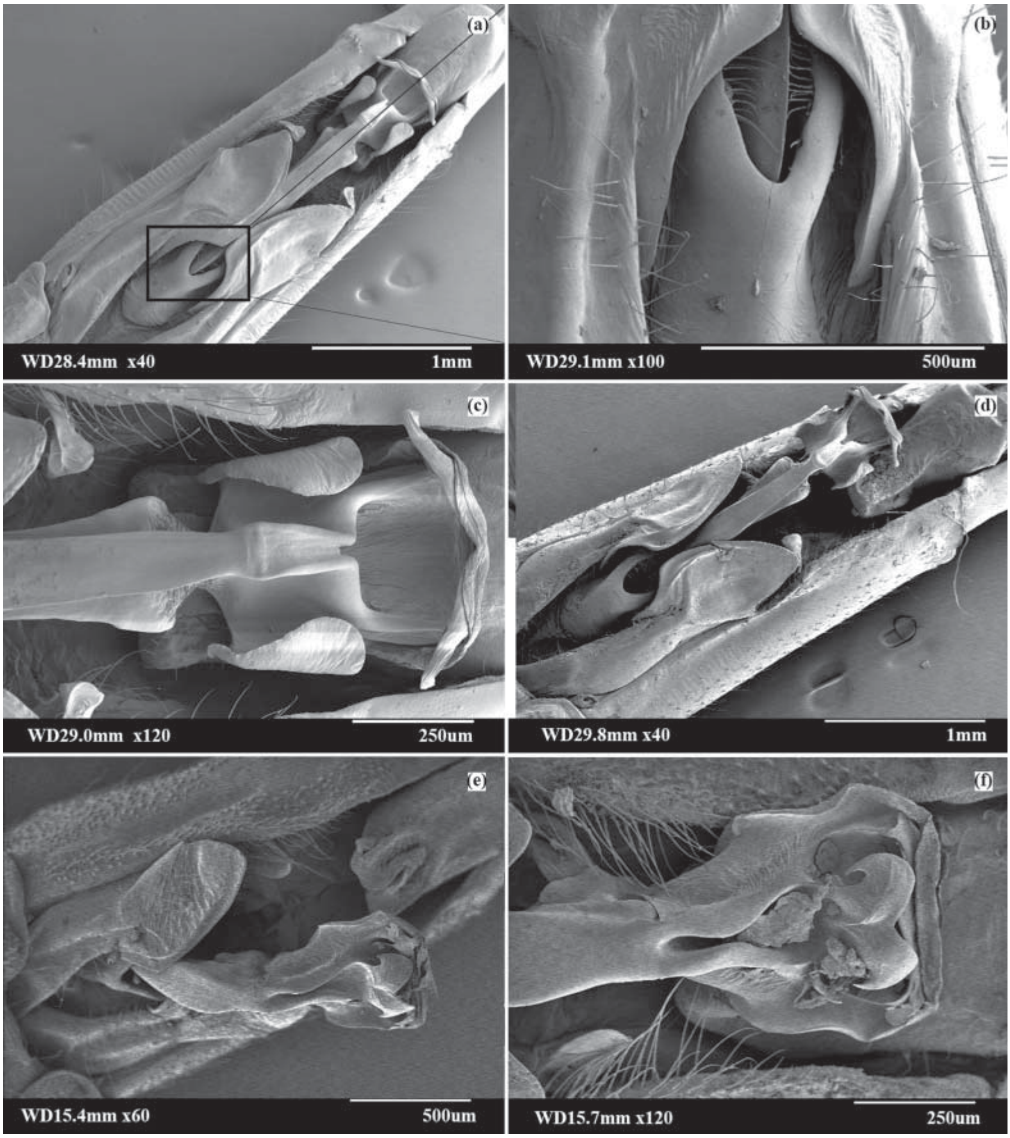

Figure 12. Male genitalia observed under scanning electron microscope. (a) Ventral view of secondary genitalia and (b) a closer view of lamina batilliformis with its pili in *Chalcolestes parvidens*. (c) Ventral view of the genital ligula in *Chalcolestes parvidens* showing the elongated horn-like structures of the shelf, the enlarged lobes laterally to the chitin stem branches and laterally to the prophallus. (d) Ventral view of the secondary genitalia in *Chalcolestes viridis*. (e) Ventrolateral view of the secondary genitalia and (f) the genital ligula in *Sympecma fusca*.

Nevertheless, the differences in the secondary genitalia support the generic status. Our findings are consistent with Pinhey's (1980): *Chalcolestes* sp. have no hood and the chitin stem branches are elongated, *Lestes* sp. and *S. fusca* have a hood with shorter chitin stem branches. Morphologically *S. fusca* is closer to *Lestes* spp. than the *Chalcolestes* species. Furthermore, the morphology of female genitalia also differs between the genera. *L. barbarus* and *L. virens* have no spermatheca and store sperm only in bursa copulatrix while *S. fusca* has one spermatheca and *C. viridis* has two small spermathecae (Uhia & Rivera, 2005).

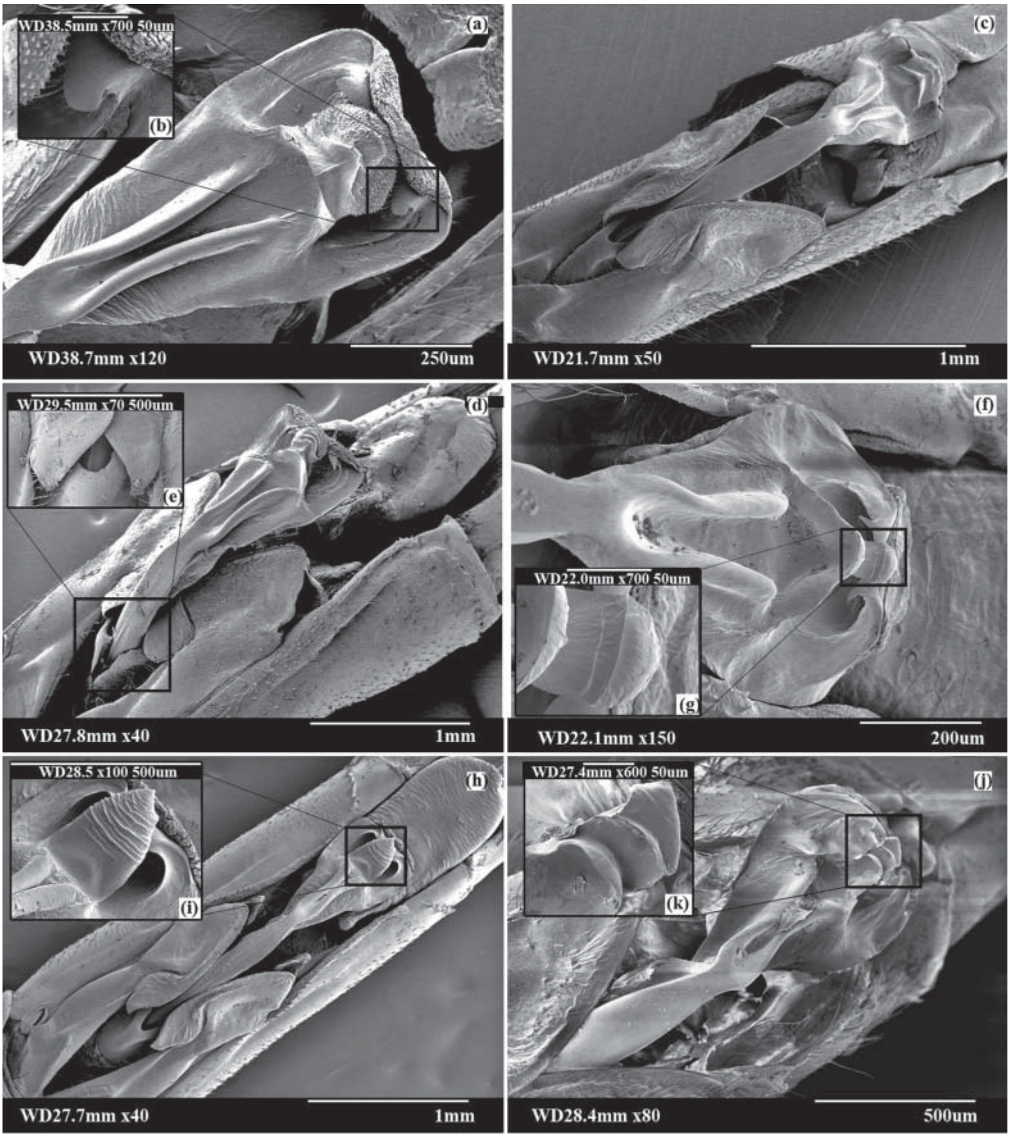

Figure 13. Male genitalia observed under scanning electron microscope. (a) Ventral view of the genital ligula with (b) a closer view of the horn-like structures of the shelf and the (c) ventral view of the secondary genitalia in *Lestes sponsa*. (d) Ventral view of the secondary genitalia and (e) a closer view of the lamina batilliformis in *Lestes dryas*. (f) Ventral view of the genital ligula and (g) the hood in *Lestes virens*. (h) Ventral view of the secondary genitalia and (i) the hood in the genital ligula in *Lestes barbarus*. (j) Ventral view of the genital ligula and (k) the hood in *Lestes macrostigma*.

Only a few works have paid attention to the morphology of secondary genitalia, especially the ligula. All species were found share the characteristic of the spoon-shaped ligula. *Lestes secula* May, 1993 (see figure 1 in May, 1993) and *Lestes disjunctus* Selys (see figures 5, 6 in Kennedy, 1920b) are very similar to the *Lestes* species in our work with the medium long chitin stem branches and a conspicuous hood in the middle of the glans. *Archilestes* species like *Archilestes neblina* Garrison, 1982 (see figures 3–6 in Garrison, 1982), *Archilestes guayarca* De Marmels, 1982 and *Archilestes tuberalatus* (Williamson) (see figures 5, 6, 10, 11 in De Marmels, 1982) and *Archilestes grandis* (Rambur) (see figures 3, 4 in Kennedy, 1920b) also have medium long

stem branches and a hood but seems to have another paired lobe next to the hood. *Austrolestes cingulatus* (Burmeister) bears a narrow hood with seemingly shorter chitin stem branches and a more angular shape of the glans (see figures 7, 8 in Kennedy, 1920b). *Indolestes tenuissimus* Tillyard, has moderately long chitin stem branches with a short shelf and a long hood that curls back under itself (see figure 9 under the name Austrolestes in Kennedy, 1920b).

Noteworthy is that Kennedy (1920a) not only described the genus *Chalcolestes* but established two other genera inside the family Lestidae, also partly on the basis of the morphology of ligula. These are the *Ceylonolestes* with the type species *Austrolestes analis* and the *Africalestes* with the type species *Lestes virgatus*. The former is the synonym of *Austrolestes* (Steinmann, 1997), the latter is the synonym of *Lestes* (Jödicke, 1997; Steinmann, 1997).

Furthermore, a trend can be seen in the structure of the secondary genitalia which refer to the northern and southern clades of genus *Lestes*. The five European species in the genus *Lestes* fall into a northern [*L. dryas*; *L. sponsa*] and a southern [*L. macrostigma*; *L. virens*; *L. barbarus*] clade (Dijkstra & Kalkman, 2012) referring to their glacial refugia (Dévai, 1976). The members of the northern clade have a wider hood instead of narrowed one and the paired horn-like structure seems to be slightly longer than in the members of the southern clade. As well, *L. dryas* and *L. sponsa* are clearly separated in most of the analyses, mainly on the basis of the measurements of the abdominal end. These differences need a detailed analysis in the future.

Overall the genital characters, especially the structure of the secondary genitalia, may reflect the relationships between species better than morphometrics in this case. Furthermore, secondary genitalia can be a good character not just at the species level (cf. Song & Bucheli, 2010) despite the fact that male genitalia evolve rapidly and divergently (Arnqvist, 1997).

The genetic data (Dijkstra & Kalkman, 2012; Dumont et al., 2010; Gyulavári et al., 2011; Samraoui, 2009) clearly placed genus *Chalcolestes* distantly from true *Lestes*. However, no phylogeny was constructed our analyses could separate the genus *Chalcolestes* form the genus *Lestes* clearly, but not distantly. Considering the results of Gyulavári et al. (2011) and Dumont et al. (2010) and our own, we find the data supportive for the generic status of *Chalcolestes*. The small size of the genus *Chalcolestes* might still be considered a problem. It is debatable whether the existence of small genera, which contain no information about relationships (Scotland & Sanderson, 2004), or large genera, which can be non-monophyletic or inconvenient, are more preferable. Thus one must choose between two possibilities: leave a monophyletic group at a given taxonomic level as a whole single unit, or subdivide the group in the same level to several smaller groups. In the family Lestidae there are nine genera with an average of 16.9 species. The most numerous genus is the *Lestes* with 84 species included, while five of the genera (*Sinhalestes*, *Chalcolestes*, *Platylestes*, *Sympecma*, *Orolestes*) have at most five species (Schorr & Paulson, 2017).

In conclusion, a detailed morphological and genetical analysis is recommended for the whole Lestidae family as, for example, Kalkman and Theischninger (2013) did with the family of Argiolestidae or Dumont, Vanfleteren, De Jonckheere, and Weekers (2005) with the Calopterygoid damselflies. Until then we recommend the use of genus *Chalcolestes*.

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References

Agüero-Pelegrin, M., Ferreras-Romero, M., & Corbet, P. S. (1999). The life cycle of *Lestes viridis* (Odonata: Lestidae) in two seasonal streams of the Sierra Morena Mountains (southern Spain). *Aquatic Insects*, *21*(3), pp. 187–196. doi:10.1076/aqin.21.3.187.4522

Arnqvist, G. (1997). The evolution of animal genitalia: Distinguishing between hypotheses by single species studies. *Biological Journal of the Linnean Society*, *60*(3), pp. 365–379. doi:10.1111/j.1095-8312.1997.tb01501.x

Artobolevsky, G. V. (1929). Strekozy Kryma. (Les Odonates de la Crimée. Odonata of Crimea). Byuleten' obschestva naturalistov i druzey prirody Kryma. *(Proceedings of the Crimean Naturalist's Society)*, *11*, pp. 139–150.

Askew, R. R. (1988). *The dragonflies of Europe* Colchester: Harley Books.

Boudot, J. P., & Kalkman, V. J. (2015). *Atlas of the European Dragonflies and Damselflies* Utrecht: KNNV Publishing.

Brauer, F. (1877). Strekosij (Odonata). In A. P. Fedtschenko (Ed.), *Reise in Turkestan Bd. 2* (pp. s1–s11): Izvestiya Imperatorskago Ljubtelej estestvoznaniya, antropol 26 (1).

Buczynski, P., & Moroz, M. D. (2008). Notes on the occurrence of some Mediterranean dragonflies (Odonata) in Belarus. *Polish Journal of Entomology*, *77*, pp. 67–74.

Bybee, S. M., Ogden, T. H., Branham, M. A., & Whiting, M. F. (2008). Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. *Cladistics*, *24*(4), pp. 477–514. doi:10.1111/j.1096-0031.2007.00191.x

Carle, F. L., Kjer, K. M., & May, M. L. (2008). Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). *Arthropod Systematics and Phylogeny*, *66*(1), pp. 37–44.

Charpentier, T. d. (1825). *Horae entomologicae, adjectis tabulis novem coloratis*. Wratislaviae: A. Gosohorsky.

Corbet, P. S. (1999). *Dragonflies: behavior and ecology of Odonata*. Colchester (UK): Harley Books.

d'Aguilar, J., Dommanget, J.-L., & Préchac, R. (1986). *A field guide to the dragonflies of Britain, Europe & North Africa*. London: William Collins Sons & Company Ltd.

Davis, R. B., Nicholson, D. B., Saunders, E. L. R., & Mayhew, P. J. (2011). Fossil gaps inferred from phylogenies alter the apparent nature of diversification in dragonflies and their relatives. *BMC Evolutionary Biology*, *11*, p 10. doi:10.1186/1471-2148-11-252

De Block, M., Geenen, S., Jordaens, K., Backeljau, T., & Stoks, R. (2005). Spatiotemporal allozyme variation in the damselfly, *Lestes viridis* (Odonata : Zygoptera): gene flow among permanent and temporary ponds. *Genetica*, *124*(2–3), pp. 137–144. doi:10.1007/s10709-005-0623-4

De Knijf, G., Vanappelghem, C., & Demolder, H. (2013). Odonata from Montenegro, with notes on taxonomy, regional diversity and conservation. *Odonatologica*, *42*(1), pp. 1–29.

De Marmels, J. (1982). *Archilestes guayaraca*, nuevo Zygoptera de Venezuela (Odonata: Lestidae). *Boletin de Entomologia Venezolana*, *2*(14), pp. 111–113.

Dévai, G. (1976). The chorological research of the dragonfly (odonata) fauna of Hungary. [A magyarországi szitakötő (Odonata) fauna chorológiai vizsgálata]. *Acta Biologica Debrecina*, *13 (Suppl. 1)*, pp. 119–157.

Dijkstra, K. D. B., & Kalkman, V. J. (2012). Phylogeny, classification and taxonomy of European dragonflies and damselflies (Odonata): a review. *Organisms Diversity & Evolution*, *12*(3), pp. 209–227. doi:10.1007/s13127-012-0080-8

Dijkstra, K. D. B., & Lewington, R. (2006). *Field guide to the dragonflies of Britain and Europe: including western Turkey and north-western Africa*. Gillingham, Dorset: British Wildlife Publishing.

Dijkstra, K. D. B., Kalkman, V. J., Dow, R. A., Stokvis, F. R., & Van Tol, J. (2014). Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology*, *39*(1), pp. 68–96. doi:10.1111/syen.12035

Dumont, H. J., Vanfleteren, J. R., De Jonckheere, J. F., & Weekers, P. H. H. (2005). Phylogenetic relationships, divergence time estimation, and global biogeographic patterns of calopterygoid damselflies (Odonata, Zygoptera) inferred from ribosomal DNA sequences. *Systematic Biology*, *54*(3), pp. 347–362. doi:10.1080/10635150590949869

Dumont, H. J., Vierstraete, A., & Vanfleteren, J. R. (2010). A molecular phylogeny of the Odonata (Insecta). *Systematic Entomology*, *35*(1), pp. 6–18. doi:10.1111/j.1365-3113.2009.00489.x

Eversmann, E. (1836). Libellulinae, Wolgam fluvium et montes Uralenses observatae. Libellulinarum species novae, quas inter Wolgam fluvium et montes Uralensis observativ Dr. Eduard Eversmann. *Bulletin Societe imperiale Naturalistes Moscou*, *9*, pp. 233, 235–248.

Fabricius, J. C. (1798). *Supplementum entomologiae systematicae*. Copenhagen: Proft & Storch.

Garrison, R. W. (1982). *Archilestes neblina*, a new damselfly from Costa Rica, with comments on the variability of *A. latialatus* Donnelly (Odonata: Lestidae). *Occasional Papers of the Museum of Zoology University of Michigan*, *702*, pp. 1–12.

Geenen, S., Jordaens, K., De Block, M., Stoks, R., & De Bruyn, L. (2000). Genetic differentiation and dispersal among populations of the damselfly Lestes viridis (Odonata). *Journal of the North American Benthological Society*, *19*(2), pp. 321–328. doi:10.2307/1468074

Grand, D., & Boudot, J.-P. (2006). *Les libellules de France, Belgique et Luxembourg* Mèze: Biotope (Collection Parthénope).

Gyulavári, H. A., Felföldi, T., Benken, T., Szabó, L. J., Miskolczi, M., Cserháti, C., . . . Dévai, G. (2011). Morphometric and molecular studies on the populations of the damselflies *Chalcolestes viridis* and *C. parvidens* (Odonata, Lestidae). *International Journal of Odonatology*, *14*(4), pp. 329–339. doi:10.1080/13887890.2011.651983 Retrieved from http://www.tandfonline.com/doi/abs/10.1080/13887890.2011.651983

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Paleontological statistics software package for education and data analysis. *Paleontologia Electronica*, *4*(1), pp. 1–9. Retrieved from http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hansemann, J. W. A. (1823). Anfang einer Auseinandersetzung der deutschen Arten der Gattung Agrion F. *Zoologisches Magazin (Wiedemann)*, *2*(1), pp. 148–161.

Hardersen, S. (2004). The dragonflies: species, phenology, larval habitats (Odonata). In P. Cerretti, S. Hardersen, F. Mason, G. Nardi, M. Tisato & M. Zapparoli (Eds.), *Invertebrati di una foresta della Pianura Padana, Bosco della Fontana, Secondo contributo* (Conservazione Habitat Invertebrati, 3rd ed., pp. 29–50). Verona: Cierre Grafica Editore.

Hardersen, S., & Dal Cortivo, M. (2008). Dragonflies (Odonata) of Vincheto di Celarda Nature Reserve, with special reference to conservation actions. In S. Hardersen, F. Mason, F. Viola, D. Campedel, C. Lasen & M. Cassol (Eds.), *Research on the natural heritage of Vincheto di Celarda and Val Tovanella (Belluno provance, Italy). Conservation of two protected areas in the context of a LIFE Project*. (Quaderni Conservazione Habitat, 5 ed., pp. 101–116). Verona: Arti Grafi che Fiorini.

Holzinger, W. E., Chovanec, A., & Waringer, J. A. (2015). Odonata (Insecta). Checklisten der Fauna Österreichs, No. 8. *Biosystematics and Ecology Series*, *31*, pp. 27–54.

Jödicke, R. (1997). *Die Binsenjungfern und Winterlibellen Europas: Lestidae* Magdeburg: Westarp Wissenschaften.

Jovic, M., Andjus, L., & Santovac, S. (2009). New data on some rare and poorly known Odonata species in Serbia. *Bulletin of the Natural History Museum in Belgrade*, *2*, pp. 95–108.

Jovic, M., Gligorovic, B., & Stankovic, M. (2010). Review of faunistical data on Odonata in Bosnia & Herzegovina. *Acta Entomologica Serbica*, *15*(1), pp. 7–27.

Kalkman, V. J., Boudot, J.-P., Bernard, R., Conze, K.-J., De Knijf, G., Dyatlova, E., . . . Sahlén, G. (2010). *European Red List of dragonflies*. Luxembourg: Publications Office of the European Union.

Kalkman, V. J., & Theischinger, G. (2013). Generic revision of Argiolestidae (Odonata), with four new genera. *International Journal of Odonatology*, *16*(1), pp. 1–52. doi:10.1080/13887890.2012.749450

Kennedy, C. H. (1920a). Forty-two hitherto unrecognized genera and subgenera of Zygoptera. *The Ohio Journal of Science*, *21*(2), pp. 83–88. doi:10.5962/bhl.part.14540

Kennedy, C. H. (1920b). The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *The Ohio Journal of Science*, *21*(1), pp. 19–32.

Kirby, W. F. (1890). *A synonimic catalogue of Neuroptera Odonata, or dragonflies. With an appendix on fossil species*. London: Gurney & Jackson.

Kis, O., Vajda, C., Gyulavári, H. A., Szabó, L. J., Miskolczi, M., Cserháti, C., & Dévai, G. (2014). A nyugati zöld rabló [*Chalcolestes viridis* (VANDER LINDEN, 1825)] egy észak-magyarországi imágópopulációjának morfológiai jellemzése. *Studia odonatologica hungarica*, *16*, pp. 5–28.

Kis, O., Vajda, C., Gyulavári, H. A., Szabó, L. J., Miskolczi, M., & Dévai, G. (2013). A keleti zöld rabló (*Chalcolestes parvidens* ARTOBOLEVSKII, 1929) egy északkelet-magyarországi imágópopulációjának morfológiai jellemzése. *Studia odonatologica hungarica*, *15*, pp. 49–72.

Kis, O., Vajda, C., Kézér, K., Szabó, L. J., Miskolczi, M., Cserháti, C., . . . Dévai, G. (2012). A nagy foltosrabló [*Lestes macrostigma* (EVERSMANN, 1836)] egy magyarországi szikes vízi imágópopulációjának morfometriai jellemzése. *Studia odonatologica hungarica*, *14*, pp. 81–102.

May, M. L. (1993). *Lestes secula*, a new species of damselfly (Odonata: Zygoptera: Lestidae) from Panama. *Journal of the New York Entomological Society*, *101*(3), pp. 410–416.

Nagy, Z., Vajda, C., Szabó, L. J., Miskolczi, M., & Dévai, G. (2012). A réti rabló (*Lestes dryas* KIRBY, 1890) hím és nőstény imágóinak morfometriai felmérése. *Studia odonatologica hungarica*, *14*, pp. 5–25.

Olias, M., & Guenther, A. (2005). First record of *Lestes* (*viridis*) *viridis* for Greece. [Erster Nachweis von *Lestes* (*viridis*) *viridis* fuer Griechenland (Odonata: Lestidae).]. *Libellula Supplement*, *6*, pp. 43–47.

Olias, M., Weihrauch, F., Bedjanic, M., Hacet, N., Marinov, M., & Salamun, A. (2007). *Lestes parvidens* and *L. viridis* in southeastern Europe: a chorological analysis (Odonata: Lestidae). *Libellula*, *26*(3–4), pp. 243–272.

Pinhey, E. C. G. (1980). A revision of the African Lestidae (Odonata). Occasional Papers of the National Museums & Monuments of Rhodesia. *Series B, Natural Sciences*, *6*(6), pp. 327–479.

Raab, R., Chovanec, A., & Pennerstorfer, J. (2007). *Libellen Österreichs* Wien: Springer-Verlag.

R Development Core Team. (2010). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rehn, A. C. (2003). Phylogenetic analysis of higher-level relationships of Odonata. [Review]. *Systematic Entomology*, *28*(2), pp. 181–239. doi:10.1046/j.1365-3113.2003.00210.x

Šácha, D., David, S., Waldhauser, M., Buczyński, P., Tończyk, G., Makomaska-Juchiewicz, M., . . . Jović, M. (2014). Draft red list of dragonflies (Odonata) of the Carpathians. In J. Kadlečík (Ed.), *Carpathian red list of forest habitats and species. Carpathian list of invasive alien species (draft)*. (pp. 172–185). Banská Bystrica: The State Nature Conservancy of the Slovak Republic.

Samraoui, B. (2009). Seasonal ecology of Algerian Lestidae (Odonata). *International Journal of Odonatology*, *12*(2), pp. 383–394. doi:10.1080/13887890.2009.9748352

Schorr, M., & Paulson, D. (2017). World Odonata List. Retrieved 2018 from http://www.pugetsound.edu/academics/academic-resources/slater-museum/biodiversity-resources/dragonflies/world-odonata-list2/.

Scotland, R. W., & Sanderson, M. J. (2004). The significance of few versus many in the tree of life. *Science*, *303*(5658), p. 643. doi:10.1126/science.1091483

Skvortsov, V. E. (2010). *The dragonflies of Eastern Europe and Caucasus: An illustrated guide*. Moscow: KMK Scientific Press Ltd.

Song, H., & Bucheli, S. R. (2010). Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. *Cladistics*, *26*, pp. 23–35. doi:10.1111/j.1096-0031.2009.00273.x

Steinmann, H. (1997). *World Catalogue of Odonata. Volume I Zygoptera*. Berlin, New York: Walter de Gruyter.

Uhia, E., & Rivera, A. C. (2005). Male damselflies detect female mating status: importance for postcopulatory sexual selection. *Animal Behaviour*, *69*, pp. 797–804. doi:10.1016/j.anbehav.2004.08.005

Vajda, C., Szabó, L. J., Miskolczi, M., Cserháti, C., & Dévai, G. (2013). A lomha rabló [*Lestes sponsa* (HANSEMANN, 1823)] egy északkelet-magyarországi imágópopulációjának morfometriai jellemzése. *Studia odonatologica hungarica*, *15*, pp. 27–47.

Vajda, C., Szabó, L. J., Miskolczi, M., & Dévai, G. (2011). A foltosszárnyjegyű rabló [*Lestes barbarus* (Fabricius, 1798)] egy északkelet-magyarországi imágópopulációjának morfometriai felmérése. *Studia odonatologica hungarica*, *13*, pp. 5–25.

Vajda, C., Szabó, L. J., Miskolczi, M., & Dévai, G. (2015a). A tavi rabló [*Lestes virens* (CHARPENTIER, 1825)] egy északkelet-magyarországi imágópopulációjának morfometriai jellemzése. *Studia odonatologica hungarica*, *17*, pp. 45–64.

Vajda, C., Vincze, A., Szabó, L. J., Miskolczi, M., & Dévai, G. (2015b). Az erdei rabló [*Sympecma fusca* (VANDER LINDEN, 1820)] egy északkelet-magyarországi imágópopulációjának morfometriai jellemzése. *Studia odonatologica hungarica*, *17*, pp. 65–83.

Vander Linden, P. L. (1820). Typographia annesii de nobilibus. *Bononiae*, pp. 1–11.

Vander Linden, P. L. (1825). *Monographiae libellulinarum europaearum specimen* Bruxelles: J. Frank.

van Tol, J. (2016). Odonata: Global Species Database of Odonata (version December 2011). Retrieved 2018 from www.catalogueoflife.org/col.

Willkommen, J., Dreyer, W., & Gorb, S. N. (2014) *Das Dilemma der Lestiden – Ökologische und funktionsmorphologische Aspekte*. Paper presented at the Jahrestagung der Gesellschaft deutschsprachiger Odonatologen, Kiel, Germany.